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ORIGINAL PAPER

Biogeographical and anthropogenic determinants of landscape-scale patterns of raptors in West African savannas

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Abstract Strong raptor population declines have recently been reported in sub-Saharan West Africa, where the pressure on wildlife and their supporting habitats is particularly high. This makes it imperative to understand the role of land-use on landscape-scale patterns of raptors and to define priority areas for conservation. We examine landscape-scale community patterns of raptors in biogeographical zones with different degrees of anthropogenic land-use and assess the role of protected areas in maintaining such patterns. We recorded raptors along road transects in Cameroon's savannas, covering four years and 7,340–7,700 km in wet and dry seasons, in three biogeographical zones: the relatively well-preserved Inundation and Guinea zones to the north and south of the heavily exploited Sudan zone. The Inundation zone had the largest species pool and Palearctic raptor richness and abundance. The Guinea zone had the largest Afrotropical raptor species pool, while raptor diversity and richness were higher there than in the Sudan zone. The abundance of only one species (Fox Kestrel) peaked in the Sudan zone and only one large-bodied raptor (Hooded Vulture) with a Sudan-centered distribution was more common there than in the other zones. Our results suggest that land-use as determined by protected areas and human exploitation may override the role of biogeographical zonation in shaping raptor assemblages. Comparable patterns of raptor richness and diversity inside and outside protected areas suggest that both protected areas and partly cultivated peripheral zones act as important foraging and source areas, ensuring the preservation of diverse raptor assemblages at the landscape scale. Finally, our data illustrate the comparatively high richness of Cameroon's and West Africa's savanna raptor communities on a continental and global scale, underlining their importance for raptor conservation.

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Introduction

The current biodiversity crisis makes it imperative to understand the role of land-use on landscape-scale patterns of biodiversity (Sinclair et al. 2002; Hoffman et al. 2010), and to minimize biodiversity loss by defining priority areas for conservation (Brooks et al. 2006; Fjeldså 2007). Raptors are among the most vulnerable taxa to environmental disturbance, and their presence often used as a proxy for high biodiversity values (Sergio et al. 2006, 2008). Strong raptor population declines have been reported throughout Africa (Thiollay 2006a, b, c, 2007a, b; Ogada and Keesing 2010; Virani et al. 2011), notably in sub-Saharan West Africa, where the pressure on wildlife and their supporting habitats is high due to some of the highest human densities and growth rates on the continent (United Nations 2011). Although West Africa's protected area network has a crucial role in maintaining raptor assemblages in the face of growing human pressure (Thiollay 2006c, 2007b), it is highly fragmented and covers a small area compared to East and southern Africa (Chape et al. 2005), potentially constraining its effectiveness for wildlife conservation (Wilkie et al. 1998; Brashares et al. 2001). Outside of protected areas, raptors have dramatically declined over vast areas of their former distribution range, some being on the brink of regional extinction (Thiollay 2006c). This is alarming given the region's importance to raptor conservation, with 69 regularly occurring species (excluding vagrants; Borrow and Demey 2001) representing 22 % of the world's raptor species, the majority (*c*. 91 %) of which seasonally dependent on West African savannas.

An understanding of biogeographical patterns of species distribution is a prerequisite for identifying priority areas and efficient protected area systems for conservation (Emanuel et al. 1992; Turpie 1995). Because rainfall is a major driver of vegetation cover and prey availability for raptors in savannas (Thiollay and Clobert 1990), raptor richness and diversity in West African savannas is centred on the Sudan savanna zone. Diversity decreases in the Sahel zone to the north because of low dry-season food supply, and in the more productive Guinea savannas to the south because dense grass cover constrains prey accessibility during the wet season (Thiollay 1977, 1978a). Within the Sudan and Sahel zones, Inundation zones offer seasonally abundant prey for Palearctic and Afrotropical raptors (Thiollay 1989; Zwarts et al. 2009), but floods and high grass cover limit prey accessibility during part of the year, reducing their suitability to most sedentary Afrotropical raptors. Currently, few long-term inventories covering wet and dry seasons have been performed to allow an assessment of the relative importance of these biogeographical zones to raptors, and how large-scale human exploitation may influence such patterns.

Our aim was to unravel the roles of biogeographical zonation and land-use in determining Palearctic and Afrotropical raptor community composition at the landscape scale in Cameroon. Significant raptor population declines in Cameroon's savannas were limited to nine out of 42 raptor species (i.e. 21 % of species declined; Thiollay 2001), whereas the majority of raptors declined significantly in central West Africa (87 %; $n = 38$ species, Thiollay 2006c), suggesting that savanna raptor populations in Cameroon had been comparably well preserved, perhaps due to an extensive protected area network (*c*. 25 % of the land surface). However, protected areas cover part of northern Cameroon's floodplains and Guinea savannas of the Bénoué Valley, whereas the densely populated Sudan savannas are little protected, raising the question whether their intensive exploitation had influenced biogeographical patterns of raptor community richness and diversity. To investigate whether this was the case, we document year-round patterns of raptor species richness, diversity, and relative abundance in the Inundation zone, Sudan savanna and Guinea savanna of Cameroon, covering 4 years and dry and wet seasons. We expect that (1) raptor abundance peaked in the Inundation zone, whose partly flooded grasslands attract high numbers of Palearctic and Afrotropical migrants; (2) protected areas in the Inundation and Guinea zones had a significantly higher raptor species diversity, species density, and richness than unprotected areas in the same zone; (3) as a consequence of their better preservation, the Guinea savannas and Inundation zones of Cameroon had a higher raptor species richness, species density, and diversity than the heavily exploited Sudan savannas; and (4) the high protected area coverage of Cameroon's savannas has ensured the preservation of a comparably rich raptor assemblage on a continent-wide and global scale.

Methods

Study area

The study area was largely located in the Far North, North and Adamawa Provinces of Cameroon (7°12′N–12°05′N and 13°′E–15°10′E; Fig. 1). The climate is semi-arid (mean annual temperature: 24–28 °C) with rains between April and October, several weeks earlier in the south. Road surveys covered three of West Africa's main biogeographical zones with distinct vegetation composition and productivity: (1) the Inundation zone is located in the Sudano-Sahelian transition zone (rainfall: 450–700 mm/annum) and supports edaphic grassland with *Acacia* and broad-leaved woodlands on flat terrain (White 1983). Agriculture includes dry-season sorghum, millet, and rice. Human population density is low (averagely 10–25 people/km^2) but has sharply increased in the past two decades (Scholte 2003). The Waza-Logone floodplains situated along the Logone River are part of the more extensive Lake Chad Basin and are partly flooded from August to November (Scholte 2005). The 1,700-km^2 Waza National Park (N.P.) protects woodlands and part of the floodplains and small populations of herbivores, but large wildlife has been virtually exterminated in the 45-km^2 Kalamaloué N.P. (Scholte 2003). (2) The Sudan zone is located in the Sudan savanna belt (rainfall: 700–1,100 mm/annum) and characterized by hilly terrain with undifferentiated Sudanian woodlands with *Isoberlinia doka*, *Balanites aegyptiaca, Piliostigma reticulatum* and *Combretum erythrophyllum* (White 1983), rising to 500–1,440 m a.s.l. in the Mandara Mountains. The entire area is relatively densely populated compared to the other zones, with averagely *c.* 50 people/km^2 (locally 350 people/km^2), with a correspondingly high rate of land conversion (Fig. 1). Sorghum, cotton, millet, maize, beans, and groundnut are the most important crops. Few patches of natural habitat remain in small (<40 km^2) and heavily exploited forest reserves and the 17-km^2 Mozogo-Gokoro N.P. (3) The Guinea zone is located in the Guinea savanna belt (rainfall: 1,100–1,600 mm/annum), with Sudanian woodland with abundant *Isoberlinia* in the north (White 1983), on undulating terrain. The Bénoué Valley encompasses a large river system and the Bénoué, Boubandjidda, and Faro N.P.s cover an area of approximately 7,600 km^2. Twenty-eight sport-hunting zones cover 16,000 km^2 and have hunting quota for larger mammals and gamefowl (Mayaka 2002). Human populations (averagely 13 people/km^2) cultivate traditional crops such as millet and increasingly cotton.

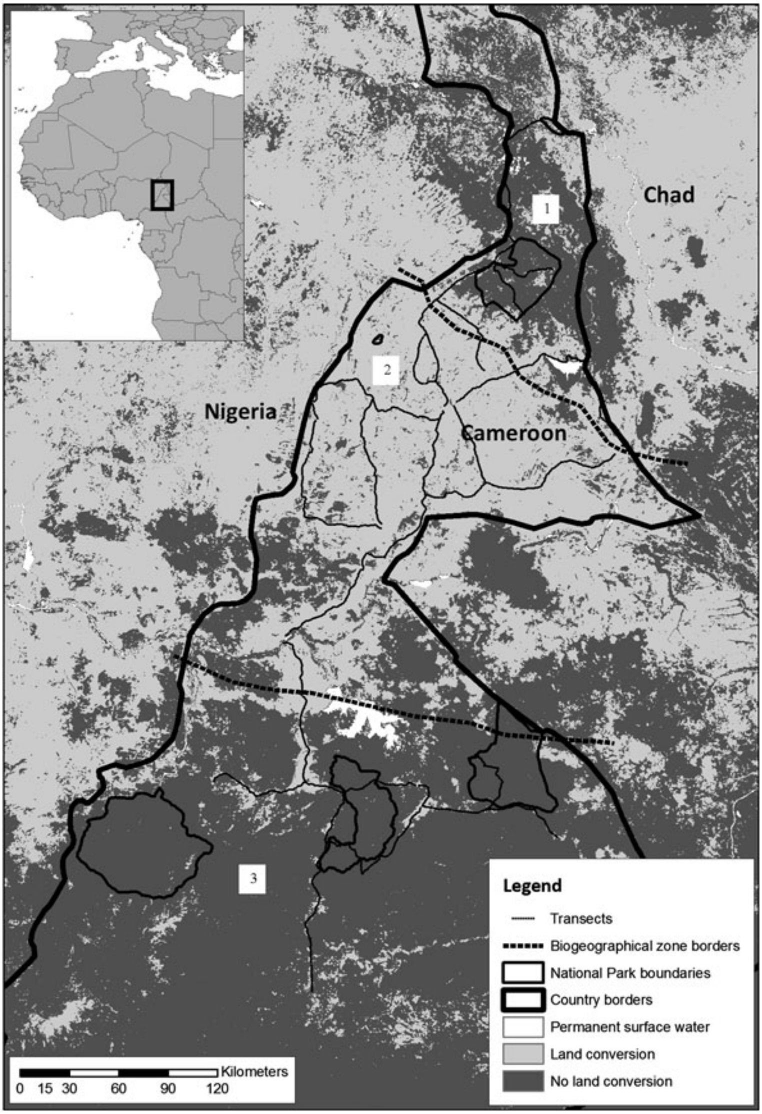

Fig. 1 Study area in Northern Cameroon. Numbers refer to the biogeographical zones: (*1*) Inundation zone, (*2*) Sudan zone, and (*3*) Guinea zone. Land cover data were based on the GlobCover Project (ESA and UCLouvain 2010). Of the 22 land cover classes in GlobCover, five classes related to human land-use conversion (post-flooding or irrigated croplands, rain-fed croplands, mosaic cropland, mosaic vegetation, and artificial surfaces and associated areas) were lumped into a single "land conversion" layer

Sampling design

A subset of navigable roads was identified for road surveys (Fig. 1), which were widely spaced and reflected gradients of human population density, topography, and land-use in each zone. Eight transects (35–115 km) were surveyed in each zone, totalling 425 km in the Inundation zone (90 km inside protected areas), 897 km in the Sudan zone (none in protected areas), and 603 km (310 km inside protected areas) in the Guinea zone. Road transects were surveyed every 6-month period between March 2007 and December 2010, four times in the dry (15 October–15 April) and four times in the wet seasons (15 April–15 October). In the Guinea zone, 90 km of the transect scheme was inaccessible during the wet season and only surveyed during the dry season. Overall, the distance covered by road surveys was 7,700 km during the dry season and 7,340 km during the wet season.

Raptors were counted by two experienced observers (one driving) from a slow-driving vehicle (average driving speed 20–25 km/h) to provide an index of relative abundance (Fuller and Mosher 1981; Bibby et al. 1992). All raptors perched or flying within eyesight range were recorded and identified with 10 × 42 binoculars. Short stops (∼20 s) were made at 1-km intervals to aid detectability of small and uncommon species, and to record habitat features. Additional stops were necessary to identify species and individuals spotted during stops were included in the counts. The position of each raptor was recorded from the vehicle with a GPS where the raptor was perpendicular to the road. Since differences in raptor detectability can confound comparisons between habitats (Millsap and LeFranc 1988), the perpendicular distance of a raptor to the road was measured with a calibrated rangefinder to establish effective strip width (ESW; Buckland et al. 1993). Surveys started at 06.30–07.30 a.m. and were conducted only with fine weather, i.e. avoiding overcast weather, rain, and strong winds. Counts were finalized before 12.30–13.30 p.m. and repeat surveys were initiated from opposite directions to reduce a time bias in raptor detectability.

We examined patterns of community composition between zones separately for Palearctic raptors, which breed north and winter south of the Sahara, and Afrotropical raptors, those breeding south of the Sahara. The breeding range of Black Kite (*Milvus migrans*), Common Kestrel (*Falco tinnunculus*) and Egyptian Vulture (*Neophron percnopterus*) extended north and south of the Sahara. For these raptors, we used the origin of the majority of individuals making up the population for diversity estimates in each zone. Individuals breeding south of the Sahara were distinguishable for Common Kestrel based on plumage differences between the Palearctic *F. t. tinnunculus* and the Afrotropical *F. t. rufescens* (Ferguson-Lees and Christie 2001). Sedentary Egyptian Vultures are associated year-round with cliffs at a known breeding site (Scholte 1998), whereas those of Palearctic origin visit the floodplains between June-November (Thiollay 1977). Individuals of Afrotropical or Palearctic origin could not be consistently distinguished for Black Kite, but the Afrotropical subspecies ("Yellow-billed Kite") greatly outnumbers Palearctic Black Kites in northern Cameroon (Thiollay 1978b).

Data analyses

Raptor counts were expressed as individuals/100 km for each species to compare estimates of relative abundance between biogeographical zones. To examine potential differences in detectability between zones which may confound such comparisons, we first determined ESW in Distance 6.0 (Thomas et al. 2006), separately for species with >40 observations per zone and for raptors of comparable size for the remaining species. Half-normal key functions with cosine and Hermite polynomial adjustment terms, hazard-rate key function with cosine and simple polynomial, and uniform key function with cosine and simple polynomial were used to model detection functions and model selection was based on the Akaike Information Criterion (AIC; Buckland et al. 1993).

Generalized Estimated Equations (GEEs; Hardin and Hilbe 2003) with robust variance estimation were used to compare relative abundance patterns in SPSS 19.0 (SPSS Inc, Chicago, IL, USA). We analyzed the data separately for the dry and wet seasons. In case of significantly different ESW between zones, we corrected relative abundance estimates by multiplying these with 1/ESW. Abundance was modelled for raptors with >10 observations and recorded in all three biogeographical zones during at least one season. The GEEs enabled the fitting of a log-linear model and permitted the assumption that the error distribution followed a Poisson or Negative Binomial distribution. Transect identity ($n = 24$) was taken as subject variable and the period in which transects were surveyed ($n = 4$ for each season) as the within-subject variable. To account for potential interannual variability, we tested two main-effects models ("biogeographical zone identity" with and without "year of survey") and a model that included these effects and their interaction. We selected the best model to describe the data based on goodness-of-fit statistics, i.e. the one with the lowest value for the quasi-likelihood under the independence model criterion (QIC; Hardin and Hilbe 2003). Differences in relative abundance between zones were tested using pair-wise comparisons and considered significant at $P < 0.05$.

For comparisons of richness and diversity estimates among biogeographical zones, we used cumulative counts on 10-km transect segments surveyed eight times in the Inundation ($n = 39$ segments), Sudan ($n = 87$), and Guinea zone ($n = 51$) as the units of replication. GPS-referenced observations were assigned to segments in ArcView GIS 3.2 (Esri 1999). We constructed sample-based rarefaction curves in EstimateS 8.0 software (Colwell 2006), using sampling without replacement, to account for differences in sampling effort among zones and to remove patchiness in the sample data by averaging values over repeated randomizations (Gotelli and Colwell 2001). Rarefaction curves were rescaled to the number of samples (i.e. transect segments) to compare species density between zones; and rescaled to the number of individuals to compare species richness (Colwell et al. 2004). We plotted the number of individuals against the number of samples to compare population density. We also computed richness estimates for segments inside protected area boundaries, i.e. National Parks, hunting zones and forest or faunal reserves, and all other, unprotected areas in the Inundation and Guinea zones. Shannon diversity estimates were calculated using sampling with replacement in EstimateS (Magurran 1988). The criterion used to determine whether the estimations of species richness, density and diversity were significantly different was the absence of overlap among the 95 % confidence intervals of the rarefaction curves (Colwell et al. 2004). Since rarefaction cannot be used to provide an estimate of asymptotic species richness, we used the mean value for seven nonparametric species estimators (ACE, ICE, Chao1, Chao2, Jackknife1, Jackknife2, bootstrap; Walther and Morand 1998) to assess sampling completeness and to estimate asymptotic or "true" species richness for each zone (Gotelli and Colwell 2001).

For comparison of raptor richness at a global scale, we searched publications and unpublished reports of similar surveys in comparable habitats which presented information on methodology, species and individuals counted. Comparisons of richness estimates were standardized based on counts of individuals (Gotelli and Colwell 2001). Since most published raptor surveys were conducted during the dry season or general "breeding season", we used the dry-season counts in northern Cameroon for these comparisons.

Results

Patterns of raptor abundance, richness and diversity

A total of 58 raptor species was identified and 16,968 individuals were detected (Table 1). Species accumulation curves (Figs. 2, 3) and species richness estimators (Table 2)

Table 1 The number of individuals counted and the percentage population composition in three biogeographical zones in northern Cameroon, during road transect surveys between 2007 and 2010

	Total count	Dry season			Wet season		
		Inundation zone	Sudan	Guinea	Inundation zone	Sudan	Guinea
Black Kite (*Milvus migrans*)	3,771	36	11	2	43	7	2
Hooded Vulture (*Necrosyrtes monachus*)	3,345	7	40	3	7	43	<1
Grasshopper Buzzard (*Butastur rufipennis*)	1,912	9	4	25	24	4	11
Fox Kestrel (*Falco alopex*)	815	<0.1	9	7	<1	11	5
Dark Chanting Goshawk (*Melierax metabates*)	724	4	4	3	4	4	6
African Swallow-tailed Kite (*Chelictinia riocourii*)	674	10	3	<1	3	1	–
Wahlberg's Eagle (*Aquila wahlbergi*)	574	1	2	6	2	6	14
Black-shouldered Kite (*Elanus caeruleus*)	567	3	3	5	2	3	10
Rüppell's Vulture (*Gyps rueppellii*)	520	1	6	2	<1	6	2
Eurasian Marsh Harrier (*Circus aeruginosus*)	491	9	<1	1	1	<0.1	–
Lanner Falcon (*Falco biarmicus*)	390	1	3	5	2	2	3
Red-necked Buzzard (*Buteo auguralis*)	295	<0.1	1	4	1	4	5
Gabar Goshawk (*Micronisus gabar*)	270	1	2	1	2	2	<1
Booted Eagle (*Hieraaetus pennatus*)	262	3	3	1	–	–	–
African white-backed Vulture (*Gyps africanus*)	195	2	<1	2	2	<0.1	3
Tawny Eagle (*Aquila rapax*)	187	2	1	1	2	1	<1
Grey Kestrel (*Falco ardosiaceus*)	182	<0.1	1	3	<1	2	6
Bateleur (*Terathopius ecaudatus*)	174	1	<0.1	4	1	<0.1	4
Common Kestrel (*Falco tinnunculus*)	174	1	2	1	–	1	–
Shikra (*Accipiter badius*)	169	<0.1	<1	5	<1	1	4
Long-crested Eagle (*Lophaetus occipitalis*)	156	<1	<0.1	5	<1	<1	6
European Snake Eagle (*Circaetus gallicus*)	119	2	1	<1	<0.1	<0.1	–
Montague's Harrier (*Circus pygargus*)	112	2	1	<1	–	–	–
Brown Snake Eagle (*Circaetus cinereus*)	107	–	1	3	<0.1	<1	4
Red-headed Merlin (*Falco chicquera*)	98	1	<1	1	1	<1	2
African Harrier Hawk (*Polyboroides typus*)	72	<1	<1	2	<1	<1	2

Table 1 continued

	Total count	Dry season			Wet season		
		Inundation zone	Sudan	Guinea	Inundation zone	Sudan	Guinea
Steppe Eagle (*Aquila nipalensis*)	57	1	<0.1	<1	<0.1	–	–
Pallid Harrier (*Circus macrourus*)	56	1	<1	<1	–	–	–
Beaudouin's Snake Eagle (*Circaetus beaudouini*)	54	<1	–	<1	1	<1	<1
African Hawk Eagle (*Hieraaetus spilogaster*)	42	<0.1	<0.1	1	<0.1	<1	1
Lapped-faced Vulture (*Torgos tracheliotus*)	40	<1	–	–	1	–	<1
Ayres's Hawk Eagle (*Hieraaetus ayresii*)	38	–	<0.1	<1	<0.1	1	1
African Fish Eagle (*Haliaeetus vocifer*)	37	<1	–	1	<1	<0.1	<1
Martial Eagle (*Polemaetus bellicosus*)	37	–	<1	1	–	<1	1
Lizard Buzzard (*Kaupifalco monogrammicus*)	36	–	<0.1	1	–	<0.1	2
Western Banded Snake Eagle (*Circaetus cinerascens*)	31	–	–	1	–	<0.1	1
Egyptian Vulture (*Neophron percnopterus*)	28	<1	<0.1	–	<0.1	<1	–
White-headed Vulture (*Trigonoceps occipitalis*)	23	<0.1	<0.1	1	<0.1	<0.1	<1
Long-legged Buzzard (*Buteo rufinus*)	22	<1	<0.1	–	–	–	–
African Cuckoo Hawk (*Aviceda cuculoides*)	20	–	–	<1	–	<1	1
Honey Buzzard (*Pernis apivorus*)	19	–	<1	<1	–	<0.1	<1
Lesser Kestrel (*Falco naumanni*)	18	<1	<0.1	–	–	–	–
Osprey (*Pandion haliaetus*)	13	<1	–	–	<0.1	–	<1
African Hobby (*Falco cuvierii*)	7	–	–	<0.1	–	<0.1	<1
Barbary Falcon (*Falco pelegrinoides*)	7	<1	–	–	<0.1	–	–
Eurasian Hobby (*Falco subbuteo*)	4	–	–	–	<0.1	–	<1
Ovambo Sparrowhawk (*Accipiter ovampensis*)	4	–	–	<1	–	–	<1
Bathawk (*Macheiramphus alcinus*)	3	–	–	<1	–	<0.1	–
Eastern Imperial Eagle (*Aquila heliaca*)	3	<0.1	–	–	–	–	–
Redfooted Falcon (*Falco vespertinus*)	3	–	<0.1	–	<0.1	–	–
Secretary Bird (*Sagittarius serpentarius*)	2	<0.1	–	–	–	–	<1
Levant Sparrowhawk (*Accipiter brevipes*)	2	–	–	–	–	–	<1

Table 1 continued

	Total count	Dry season			Wet season		
		Inundation zone	Sudan	Guinea	Inundation zone	Sudan	Guinea
Peregrine Falcon (*Falco peregrinus*)	2	<0.1	<0.1	–	–	–	–
Red-thighed Sparrowhawk (*Accipiter erythropus*)	1	–	–	<0.1	–	–	–
Common Buzzard (*Buteo buteo*)	1	<0.1	–	–	–	–	–
Eleonora's Falcon (*Falco eleonorae*)	1	–	–	–	–	–	<1
Lesser Spotted Eagle (*Aquila pomarina*)	1	<0.1	–	–	–	–	–
Sooty Falcon (*Falco concolor*)	1	–	–	–	–	<0.1	–
Unidentified raptors	122						

The percentage composition relative to total numbers is presented separately for the three biogeographical zones and for dry and wet seasons

indicated that the raptor surveys were almost complete. The proportion of the "true" raptor species richness observed ranged from 85 % in the Inundation zone to 96 % in the Sudan zone (Table 2), but was estimated to be more complete for Afrotropical (94–98 %) than for Palearctic raptor species (72–89 %). The Inundation zone had the highest estimated mean asymptotic total raptor richness and Palearctic raptor richness (Table 2), whereas asymptotic richness for Afrotropical raptors only was highest in the Guinea zone.

Overlap of the 95 % confidence intervals of rarefaction curves showed that differences in raptor species density were not significantly different between zones (Fig. 2a), but raptor richness was significantly higher in the Guinea zone than in the Sudan zone (Fig. 2b). The diversity of the entire raptor community, and of Afrotropical raptors, also peaked in the Guinea zone (Fig. 4). The richness of the Afrotropical raptor assemblage decreased significantly with increasing latitude (Guinea > Sudan > Inundation; Fig. 2e), but Afrotropical species density did not significantly differ between zones. Palearctic raptor species density was significantly higher in the Inundation compared to the Sudan zone (Fig. 3a), but Palearctic raptor richness and diversity did not significantly differ between zones (Figs. 3b, 4).

Population density was highest in the Inundation zone, intermediate in the Sudan zone and lowest in the Guinea zone, for both Afrotropical and Palearctic raptors (Figs. 2c, f, 3c). Dry-season population density surpassed wet-season density in all zones (not shown). At the specific level, seven Palearctic raptors recorded in three biogeographical zones reached their maximum relative abundance in the Inundation zone during the dry season (Table 3). Twenty-six Afrotropical raptors were recorded in three biogeographical zones during at least one season; the abundance of 27 and 31 % of these species peaked in the Guinea or Inundation zone, respectively, during one or both seasons (Table 3). Fox Kestrel (*Falco alopex*) was the only species most commonly recorded in the Sudan zone, during the wet season (Table 3). Seven large-bodied raptors (i.e. eagles and vultures; Table 3), were more abundant in the Inundation or Guinea zones than in the Sudan zone during one or both seasons. Only one large-bodied raptor, Hooded Vulture (both seasons), and a small eagle, Ayres's Hawk Eagle (*Hieraaetus ayresii*; wet season), were more common in the Sudan zone than the Inundation or Guinea zones (Table 3).

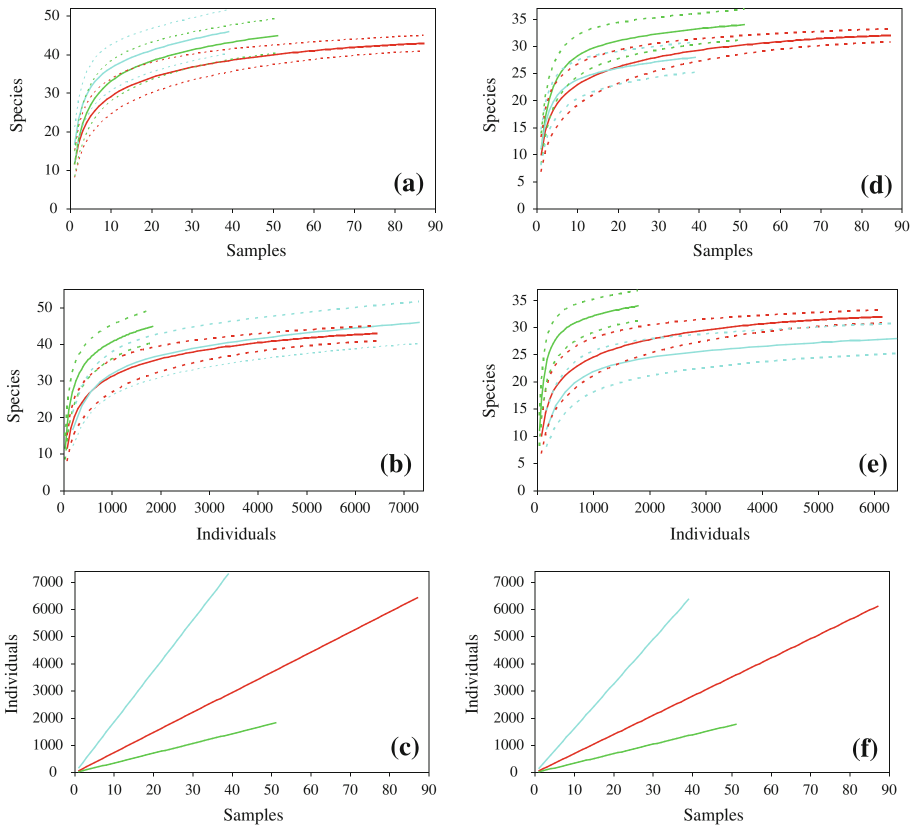

Fig. 2 Sample-based rarefaction curves (*dotted lines* indicate 95 % confidence intervals) of total raptor richness (**a**–**c**) and Afrotropical raptor richness (**d**–**f**) for the Inundation (*blue*), Sudan (*red*), and Guinea zone (*green*) in north Cameroon comparing species density (**a**, **d**), species richness (**b**, **e**) and population density (**c**, **f**). (Color figure online)

Richness and diversity in protected and unprotected areas

Rarefaction curves demonstrated no significant differences in richness, density and diversity of Afrotropical and Palearctic raptors between protected and unprotected areas in the Inundation and Guinea zones (Figs. 5, 6). Estimates of true species richness were significantly higher in unprotected areas than protected areas in the Inundation zone, for Afrotropical and Palearctic raptors (Table 2). Population density for Afrotropical raptors was higher inside protected areas (Fig. 5f). Conversely, in the Guinea zone, the estimated species pool of Afrotropical and Palearctic raptors was significantly lower in unprotected than protected areas (Table 2), but population density of Afrotropical raptors was lower inside than outside protected areas (Fig. 5c).

Comparisons with regional, continental and global raptor richness

Most studies (one exception) conducted elsewhere in West Africa generated species richness estimates within the 95 % confidence limits of our cumulative species richness

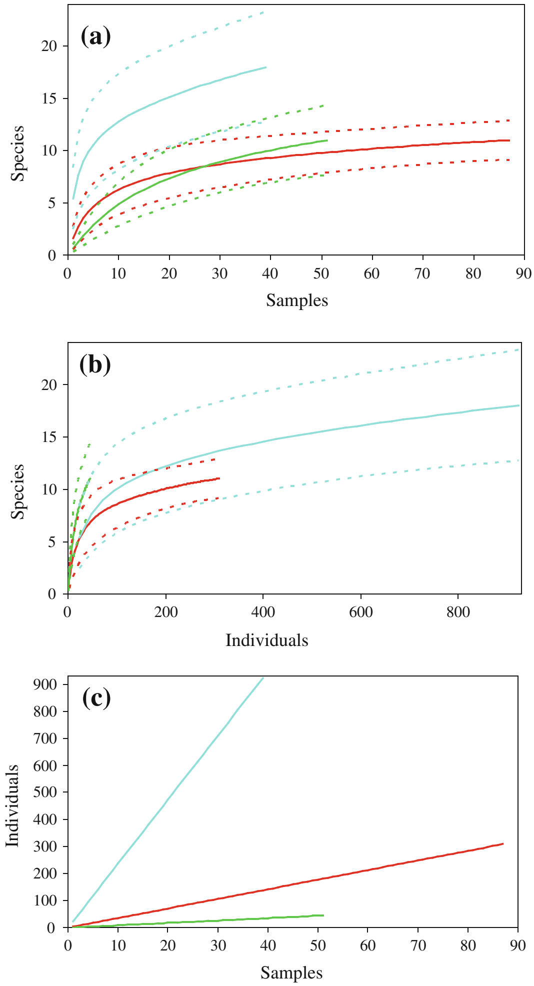

Fig. 3 Sample-based rarefaction curves (*dotted lines* indicate 95 % confidence intervals) of Palearctic raptor richness for the Inundation (*blue*), Sudan (*red*), and Guinea zones (*green*) in north Cameroon comparing species density (**a**), species richness (**b**) and population density (**c**). (Color figure online)

curve (Fig. 7), indicating comparable richness to northern Cameroon. Conversely, raptor richness estimates from similarly open habitats in South America, Asia, and southern Africa were below and outside the 95 % confidence limits of the richness curve for Cameroon. Raptor richness in the savannas of Cameroon was thus representative for the region, but relatively high on a continental and global scale, surpassed only by raptor richness in East African savannas.

Discussion

We detected distinct patterns of raptor abundance, richness and diversity in relationship to the biogeographical zones that together represent Cameroon's savanna region. Although raptor species density was generally comparable between zones, population density and the true species pool was largest in the Inundation zone. The productive, partly inundated

Table 2 Mean values (±95 % confidence intervals) for nonparametric species richness estimators (ACE, ICE, Chao1, Chao2, Jack1, Jack2, Bootstrap) for all raptors, Afrotropical, and Palearctic raptors in the Inundation (I), Sudan (S), and Guinea (G) zones of northern Cameroon, and for protected (PROT) and unprotected (UNPROT) areas in the Inundation and Guinea zones

Raptor group	Samples	Individuals (computed)	Sobs (Mao Tau)	Mean richness	% Sobs
Richness in biogeographical zones					
Raptors-I	39	7,303	46	54.2 ± 2.1	84.9
Raptors-S	87	6,432	43	45.0 ± 0.8	95.5
Raptors-G	51	1,828	45	49.7 ± 2.1	90.5
Afrotropical-I	39	6,379	28	29.9 ± 0.9	93.7
Afrotropical-S	87	6,123	32	32.7 ± 0.7	97.9
Afrotropical-G	51	1,783	34	35.8 ± 0.9	95.0
Palearctic-I	39	924	18	24.9 ± 2.3	72.3
Palearctic-S	87	309	11	12.3 ± 0.5	89.1
Palearctic-G	51	45	11	13.7 ± 1.4	80.5
Richness in protected and unprotected areas					
Raptors-I-PROT	9	2,345	39	45.9 ± 3.2	85.0
Raptors-I-UNPROT	30	4,958	42	54.3 ± 4.5	77.3
Afrotropical-I-PROT	9	2,128	25	28.4 ± 1.5	88.1
Afrotropical-I-UNPROT	30	4,251	27	32.9 ± 2.6	82.0
Palearctic-I-PROT	9	217	14	16.3 ± 0.7	86.1
Palearctic-I-UNPROT	30	707	15	21.8 ± 2.0	68.8
Raptors-G-PROT	31	855	40	48.9 ± 2.8	81.9
Raptors-G-UNPROT	20	973	36	39.2 ± 1.7	91.8
Afrotropical-G-PROT	31	844	34	37.6 ± 1.5	90.4
Afrotropical-G-UNPROT	20	939	29	31.6 ± 1.5	91.8
Palearctic-G-PROT	31	11	6	9.8 ± 1.7	61.5
Palearctic-G-UNPROT	20	34	7	7.5 ± 0.3	93.9

The proportion of species detected by surveys is presented (% Sobs)

grasslands and fringing woodlands in this zone supported the bulk of the raptor populations, again underlining their importance to Palearctic and Afrotropical raptors (Thiollay 1978b, 1989; Buij and Croes 2013). As predicted, raptor diversity and richness was not centred on the heavily exploited Sudan savanna zone, previously cited as the core biogeographical zone for the West African raptor assemblage, with the highest species diversity and richness (Thiollay 1977). Instead, raptor diversity was highest in the dense, relatively well-preserved Guinea savannas and raptor richness higher there than in the Sudan zone, largely reflecting patterns of community richness and diversity of the Afrotropical raptor assemblage. We found that only one Afrotropical raptor (Fox Kestrel) with a distribution range centered on the Sudan zone also attained its highest abundance there, while approximately a third of Afrotropical species detected in all three zones were most abundant in the Inundation or Guinea zones during all or part of the year. These included six Afrotropical large-bodied raptors with a distribution range centered on the Sudan zone: African Hawk Eagle (*Hieraaetus spilogaster*), Brown Snake Eagle (*Circaetus cinereus*), African White-backed Vulture (*Gyps africanus*), Wahlberg's Eagle (*Aquila wahlbergi*),

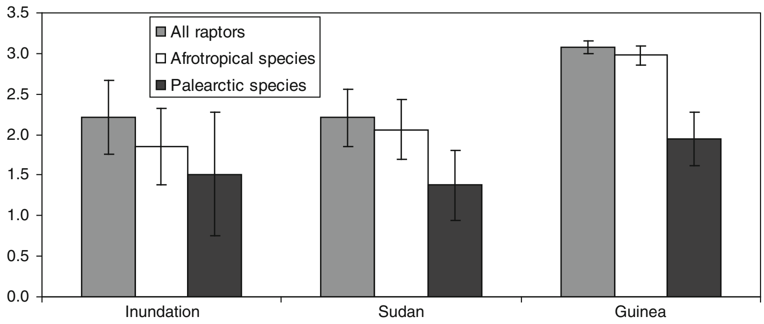

Fig. 4 Shannon diversity indices (with 95 % confidence intervals) for all raptors, Afrotropical raptors, and Palearctic raptors detected in the Inundation zone (I), Sudan zone (Su), and Guinea zone (G), in northern Cameroon. Diversity indices were estimated at approximately equal sampling effort ($n = 1{,}837$–$1{,}848$ individuals for "all raptors", $n = 1{,}772$–$1{,}795$ for "Afrotropical species", $n = 42$–47 for "Palearctic raptors")

White-headed Vulture (*Trigonoceps occipitalis*), and Bateleur (*Terathopius ecaudatus*). The human-commensal Hooded Vulture, strongly associated with numerous human settlements in the Sudan zone, was the only exception among large-bodied raptors in this regard. These results contrast with general patterns of species abundance, which tends to decline in peripheral areas of distribution ranges (Brown et al. 1995) where conditions are less favorable (Pulliam 2000; García and Arroyo 2001) and sensitivity to habitat alteration higher (Swihart et al. 2003), suggesting that human-induced habitat modification influenced raptor communities at the landscape scale, leading to greater abundance within potentially suboptimal habitat at the periphery of distribution ranges. It further suggests that extensive habitat modification resulting from anthropogenic land-use may override the dominant role of biogeographical zonation in shaping community patterns in African raptor assemblages.

Raptor richness and diversity in protected and unprotected areas

Contrary to expectations, we did not detect significant differences in raptor richness, species density, and diversity in unprotected compared to protected areas in the Inundation and Guinea zones. This may have been partly related to the use of non-overlap of 95 % confidence intervals as a criterion of statistical difference, which is generally considered overly conservative (Payton et al. 2004), although it is the most appropriate criterion currently available for rarefaction curves (Colwell et al. 2012). Our transect coverage inside human-encroached forest reserves and hunting concessions was insufficiently extensive to examine whether these protected areas had a lower raptor richness than the more effectively protected National Parks (cf. Thiollay 2007a), potentially reducing the difference in community composition with unprotected areas. However, this did not play a role in the Inundation zone, where the entire protected area network had the status of National Park. Rather, the wide-ranging habits of raptors and relative proximity of protected and unprotected areas might have reduced landscape-scale differences in raptor richness and diversity, because raptors breeding in protected areas may regularly forage over the surrounding cultivated areas. Furthermore, the open, moderately cultivated woodlands and grasslands surrounding northern Cameroon's protected areas

Table 3 Relative abundance (N/100 km) of Palearctic and Afrotropical raptors recorded during road transect surveys performed in three biogeographical zones in northern Cameroon between February 2007 and December 2010

	Dry season						Wet season					
	Inundation zone		Sudan		Guinea		Inundation zone		Sudan		Guinea	
Afrotropical raptors												
African Fish Eagle	1.77	± 1.69	–	–	0.30	± 0.23	0.25	± 0.16	0.03	± 0.04	0.35	± 0.27
African Harrier Hawk	0.36^{a}	± 0.18	0.18^{a}	± 0.14	1.20^{b}	± 0.21	0.41^{a}	± 0.19	0.39^{ab}	± 0.14	0.94^{b}	± 0.25
Bateleur	1.88^{ab}	± 1.07	0.04^{a}	± 0.03	2.39^{b}	± 0.83	4.42^{ab}	± 3.27	0.07^{a}	± 0.07	3.22^{b}	± 1.12
Hooded Vulture	26.2^{a}	±12.9	34.9^{a}	± 6.75	1.38^{b}	± 1.28	23.6^{ab}	± 16.8	38.8^{a}	± 7.42	0.20^{b}	± 0.12
White-headed Vulture	0.14	± 0.14	0.04	± 0.05	0.29	± 0.21	0.19^{a}	± 0.13	0.03^{a}	± 0.03	0.53^{b}	± 0.25
African white-backed Vulture	5.11^{a}	± 3.19	0.14^{b}	± 0.11	0.81^{b}	± 0.58	5.39	± 3.75	0.07	± 0.05	1.65	± 0.78
Rüppell's Vulture	4.19	± 2.26	6.6	± 4.42	0.26	± 0.21	1.68	± 0.84	6.45	± 3.71	1.41	± 1.13
Lapped-faced Vulture	1.56	± 0.85	–	–	–	–	1.62	± 0.72	–	–	0.13	± 0.10
Black Kite[A]	107.7^{a}	± 29.9	6.70^{b}	± 2.18	3.05^{b}	± 2.12	43.10^{a}	± 15.0	9.15^{b}	± 3.14	2.14^{c}	± 0.86
Beaudouin's Snake Eagle	0.54	± 0.28	–	–	0.13	± 0.09	1.87	± 1.00	0.23	± 0.09	0.36	± 0.16
Brown Snake Eagle	–	–	0.55	±0.17	1.77	± 0.62	0.08^{a}	± 0.08	0.29^{a}	± 0.11	2.43^{b}	± 0.66
Western Banded Snake Eagle	–	–	–	–	0.57	± 0.21	–	–	0.03	± 0.03	0.62	± 0.14
Black-shouldered Kite	9.85^{a}	± 2.63	3.22^{b}	± 0.92	2.87^{b}	± 1.12	5.94^{a}	± 1.01	2.39^{b}	± 0.42	4.57^{ab}	± 1.30
African Swallow-tailed Kite	42.54^{a}	± 26.9	2.55^{b}	± 1.30	0.08^{c}	± 0.08	5.59	± 2.28	1.06	± 0.81	–	–
African Cuckoo Hawk	–	–	–	–	0.12	± 0.09	–	–	0.13	± 0.08	0.55	± 0.17
Shikra	0.31^{a}	± 0.17	0.28^{a}	± 0.13	2.43^{b}	± 0.88	0.62^{a}	± 0.22	1.02^{b}	± 0.30	2.06^{b}	± 0.65
Gabar Goshawk	4.17^{a}	± 1.10	2.05^{a}	± 0.74	0.67^{b}	± 0.39	3.39^{a}	± 0.63	1.79^{b}	± 0.45	0.67^{b}	± 0.54
Lizard Buzzard	–	–	0.02	± 0.02	0.46	± 0.28	–	–	0.04	± 0.03	1.09	± 0.32
Dark Chanting Goshawk**	15.15^{a}	± 3.75	4.58^{b}	± 1.41	1.80^{c}	± 0.60	10.6^{a}	± 2.36	3.90^{b}	± 1.11	2.73^{b}	± 0.80
Grasshopper Buzzard**	29.56^{a}	± 8.13	3.57^{b}	± 0.93	15.3^{ab}	± 6.22	56.4^{a}	± 15.5	3.91^{b}	± 1.00	6.23^{b}	± 2.15

Table 3 continued

	Dry season						Wet season					
	Inundation zone		Sudan		Guinea		Inundation zone		Sudan		Guinea	
Red-necked Buzzard**	0.38^{a}	± 0.31	1.10^{ab}	± 0.45	2.45^{b}	± 0.81	1.44^{a}	± 0.59	4.27^{b}	± 1.15	2.14^{ab}	± 1.16
Wahlberg's Eagle	3.78^{a}	± 0.84	1.51^{b}	± 0.55	3.26^{ab}	± 1.04	4.52	± 0.89	5.07	± 1.11	5.23	± 1.27
Tawny Eagle	5.87	± 2.35	0.60	± 0.18	0.86	± 0.38	4.38	± 2.86	0.50	± 0.14	0.24	± 0.12
Martial Eagle	–	–	0.09	± 0.05	0.68	± 0.15	–	–	0.33	± 0.15	0.72	± 0.31
Long-crested Eagle	1.17^{a}	± 0.52	0.09^{b}	± 0.07	2.59^{c}	± 0.53	0.98^{ab}	± 0.63	0.09^{a}	± 0.06	2.77^{b}	± 0.56
Ayres's Hawk Eagle	–	–	0.06	± 0.05	0.34	± 0.19	0.07^{a}	± 0.07	0.45^{b}	± 0.16	0.55^{b}	± 0.18
African Hawk Eagle	0.07^{a}	± 0.07	0.08^{a}	± 0.07	0.69^{b}	± 0.22	0.08^{a}	± 0.08	0.14^{a}	± 0.12	0.82^{b}	± 0.35
Common Kestrel[B]	–	–	0.41	± 0.31	0.04	± 0.05	–	–	0.41	± 0.37	–	–
Fox Kestrel	0.07^{a}	± 0.06	7.24^{b}	± 2.87	3.06^{b}	± 1.58	0.74^{a}	± 0.50	9.48^{b}	± 3.89	2.45^{a}	± 0.92
Lanner Falcon	4.26	± 0.94	2.48	± 0.72	2.92	± 0.59	4.55^{a}	± 1.22	1.79^{b}	± 0.55	1.44^{b}	± 0.30
Grey Kestrel	0.16^{a}	± 0.16	0.58^{a}	± 0.24	1.77^{b}	± 0.46	0.36^{a}	± 0.31	1.48^{b}	± 0.32	3.35^{c}	± 1.00
Red-headed Merlin	3.21	± 2.42	0.30	± 0.17	0.48	± 0.13	1.93^{a}	± 0.86	0.17^{b}	± 0.08	0.62^{a}	± 0.19
Palearctic raptors												
Osprey	0.66	± 0.45	–	–	–	–	0.2	± 0.16	–	–	0.04	± 0.05
Egyptian Vulture[D]	2.02	± 1.88	–	–	–	–	0.23	± 0.16	–	–	–	–
Eurasian Marsh Harrier	22.9^{a}	± 5.37	0.44^{b}	± 0.17	0.62^{b}	± 0.21	0.32	± 0.20	0.03	± 0.04	–	–
Pallid Harrier	3.22^{a}	± 1.21	0.33^{b}	± 0.28	0.13^{b}	± 0.06	–	–	–	–	–	–
Montagu's Harrier	5.19^{a}	± 1.80	1.18^{b}	± 0.42	0.35^{c}	± 0.23	–	–	–	–	–	–
European Snake Eagle	4.87^{a}	± 1.23	0.73^{b}	± 0.38	0.23^{b}	± 0.23	0.06	± 0.05	0.03	± 0.02	–	–
Honey Buzzard	–	–	0.19	± 0.11	0.23	± 0.10	–	–	0.07	± 0.05	0.36	± 0.20
Long-legged Buzzard	1.64	± 1.34	0.03	± 0.04	–	–	–	–	–	–	–	–
Steppe Eagle	3.74^{a}	± 2.03	0.02^{b}	± 0.02	0.10^{b}	± 0.10	0.08	± 0.08	–	–	–	–

Table 3 continued

	Dry season						Wet season					
	Inundation zone		Sudan		Guinea		Inundation zone		Sudan		Guinea	
Booted Eagle	9.26[a]	± 3.16	3.91[b]	± 1.34	0.37[b]	± 0.13	–	–	–	–	–	–
Common Kestrel[C]	6.11[a]	± 1.66	1.69[b]	± 0.47	0.67[b]	± 0.28	–	–	–	–	–	–
Lesser Kestrel	0.84	± 0.32	0.04	± 0.04	–	–	–	–	–	–	–	–

Mean values for transects in each zone ($n = 8$) are presented ±SE. The association between biogeographical zones and relative abundance was investigated separately for each season with Generalized Estimating Equations. Lower case letters (a, b, c) indicate differences in relative abundance between zones ($P < 0.05$) using pair-wise comparisons

** Estimated strip width significantly greater ($P < 0.05$) in Inundation zone and Sudan savanna compared to Guinea savanna; significant differences in relative abundance between zones as presented here not affected after correction

[A] The majority of Black Kites referred to Afrotropical Yellow-billed Kites (*M. m. parasitus/aegyptius*; Johnson et al. 2005); *c.* < 1 % of dry season counts referred to the Palearctic race *migrans*

[B] Only includes the Afrotropical race *F.t. rufescens*

[C] Excluding local breeders

[D] Only includes the Palearctic race *F.t. tinnunculus*

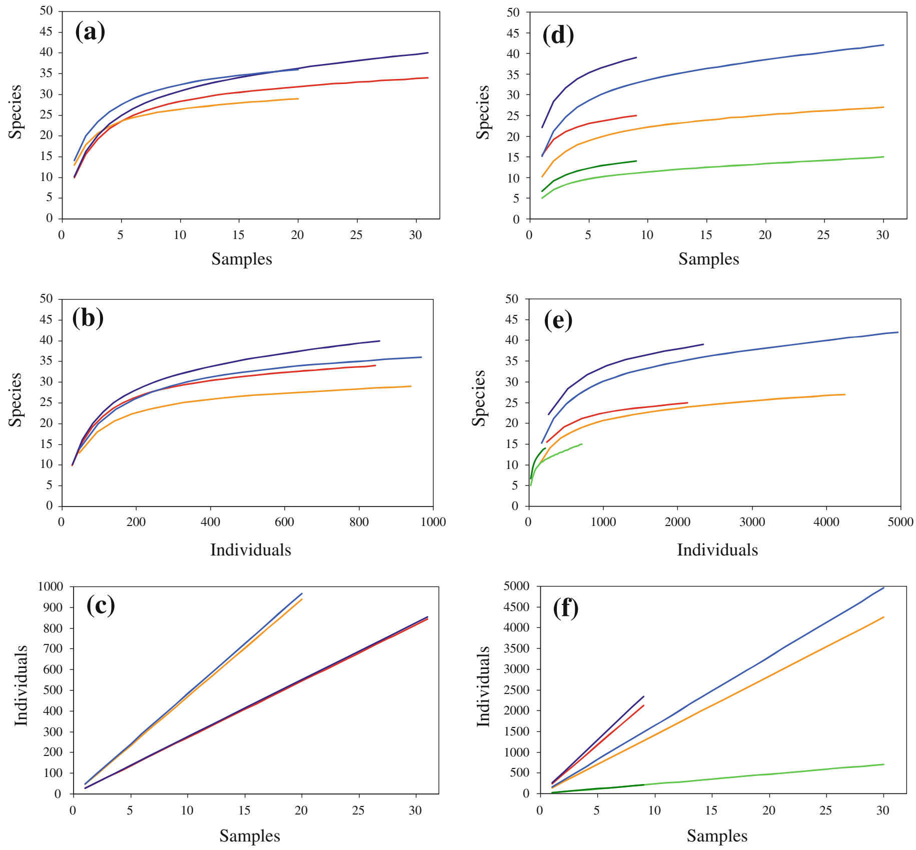

Fig. 5 Sample-based rarefaction curves of total (*blue*), Afrotropical (*red*/*orange*), and Palearctic (*green*) raptor richness for the Guinea (**a**–**c**) and Inundation zone (**d**–**f**) in north Cameroon comparing species density, species richness and population density in protected (*dark blue*, *red*, *dark green*) and unprotected areas (*light blue*, *orange*, *light green*). Numbers of Palearctic raptors were too low for comparative analyses in the Guinea zone and are shown only for the Inundation zone. The 95 % confidence intervals (not shown) overlapped for every pair of curves pertaining to the same species sub-group

provide suitable nest and foraging habitat for various Afrotropical and Palearctic raptors (Buij et al. 2012, 2013a, b), partly explaining the greater raptor population density (Guinea zone) and species pool (Inundation zone) in the unprotected areas. These results suggest that protected areas and their human-transformed peripheral zones may together function as important foraging and source areas for Palearctic and Afrotropical raptor populations, ensuring the preservation of rich and diverse raptor assemblages at the landscape scale.

Comparisons with regional, continental and global raptor richness

Our data illustrated the comparatively high richness of Cameroon's and West Africa's savanna raptor community, on a continental and global scale. Obviously, caution is

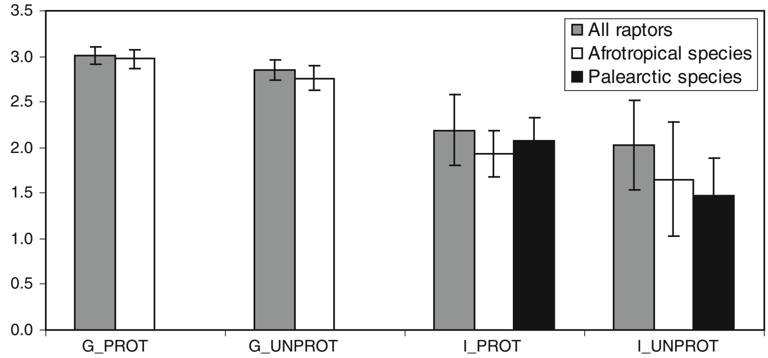

Fig. 6 Shannon diversity indices for all raptors, Afrotropical raptors, and Palearctic raptors in protected (PROT) and unprotected (UNPROT) areas of the Inundation zone (I), and Guinea savanna (G) in north Cameroon. Numbers of Palearctic migrants in the Guinea zone were too low for accurate comparisons and were left out. Indices were estimated at approximately equal sampling effort ($n = 772$–860 individuals for "all raptors", $n = 839$–942 for "Afrotropical species", $n = 210$–217 for "Palearctic raptors"). Values are presented with 95 % confidence intervals

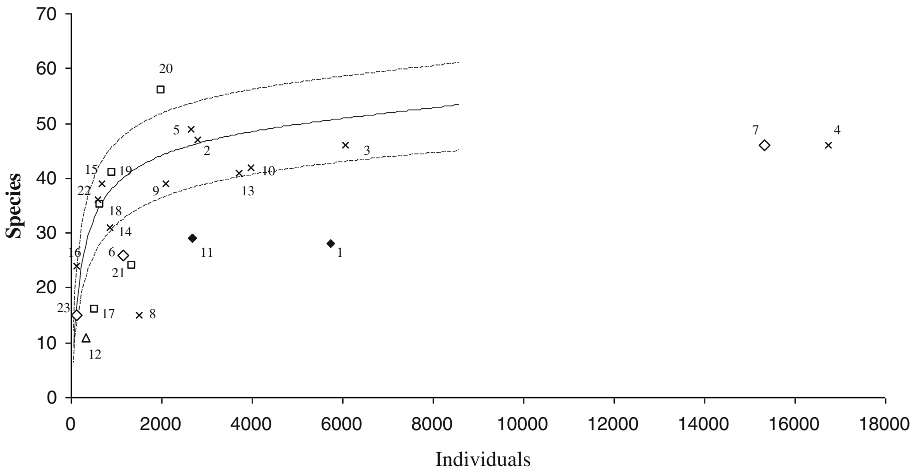

Fig. 7 Raptor richness accumulation curve (with 95 % confidence intervals) based on 7,080 km dry-season road transect surveys in northern Cameroon between 2007 and 2010, compared to raptor richness recorded on road surveys in similar habitats in West Africa (*times*), East Africa (*unfilled square*), southern Africa (*unfilled diamond*), South America (*filled diamond*), and Asia (*unfilled triangle*). Numbers refer to published records (see Appendix)

needed when comparing richness estimates between widely spaced localities differing in ecosystem productivity, topographical and vegetational diversity, since raptor richness is influenced by such parameters (Sergio et al. 2006, 2008). However, other studies used similar methods and incorporated similarly diverse, partly protected areas (see Appendix), justifying our comparative assessment. Apart from the significant importance of the floodplains as a wintering area for various Palearctic raptor species, others routinely stop-over in the region en route to and from their wintering range at more southerly latitudes (e.g. Hake et al. 2003; Gschweng et al. 2008), contributing to the diverse and highly dynamic raptor assemblage that characterizes this region.

Conservation concerns

The protected area network in northern Cameroon incorporates two main biogeographical zones that support a large portion of West Africa's savanna raptor species during much of the year, which may have been instrumental in maintaining much of the integrity of its raptor community. Contrary to the situation elsewhere in the region (Thiollay 2006c), we found that large-bodied raptors still persist at low densities in the heavily exploited Sudan zone, implying connectivity between populations inside protected areas to the north and south, an important prerequisite for population viability. On the other hand, various large raptors formerly encountered regularly in Cameroon's Inundation zone, such as Martial Eagle (*Polemaetus bellicosus*), White-headed and *Gyps* vultures (Louette 1981; Mundy et al. 1992; Scholte 1998; Scholte et al. 1999) have now become rare and appear to have suffered most under agricultural development initiatives and increased human pressure in the area (Buij and Croes 2013). Like other small protected areas (<2,500 km^2) in the region where strong declines of large raptors have been reported (Thiollay 2000, 2006c; Rondeau et al. 2008; Tende and Ottosson 2008), Waza N.P. may not be sufficiently large to maintain viable populations of disturbance-sensitive, large raptors, whereas larger protected areas (>4,000 km^2) do seem to retain this group (e.g., Salewski 2000; Thiollay 2006c; Dowsett-Lemaire and Dowsett 2008). This suggests that protected area-size may be of vital importance to the long-term persistence of large raptors, as reported for other wildlife (Brashares et al. 2001), and further studies are urgently needed to identify the causes for raptor decline inside the region's protected areas.

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Appendix

See (Table 4).

Table 4 List of published and unpublished reports of raptor richness estimated using road transects

Number	References	Country	Habitat	Coverage[a]	Years	Season
1	Jensen et al. (2005)	Venezuela	Wetlands, agriculture, forests	Region	2000–2002	Dry and wet
2	Rondeau et al. (2008)	Guinea	Guinea and Sudan savannas, protected area	Region	2006	Dry
3	Thiollay (2006c)	Burkina Faso, Mali and Niger	Floodplain, Sahel and Sudan savannas, protected area	Region	2003–2004	Dry
4	Thiollay (2006c)	Burkina Faso, Mali and Niger	Floodplain, Sahel and Sudan savannas, protected area	Region	1969–1973	Dry
5	Thiollay (1975a)	Chad	Sudan savanna, protected area	Local	1973	Dry
6	Cade (1969)	South Africa	Woodland savanna, protected area	Local	1959–1965	Wet
7	Herremans and Herremans-Tonnoeyr (2000)	Botswana	Woodland savanna, protected area	Region	1991–1995	Dry and wet
8	Anadón et al. (2010)	Mauritania, Mali	Sahel savannas	Region	2004	Dry
9	Thiollay (2001)	Cameroon	Floodplain, Sudan savanna, protected area	Region	2000	Dry
10	Thiollay (2001)	Cameroon	Floodplain, Sudan savanna, protected area	Region	1973	Dry
11	Carrete et al. (2009)	Argentina	Forest, floodplain, grasslands, woodland, mountain forest, desert	Region	2002–2005	Breeding season
12	Sanchez-Zapata et al. (2003)	Kazakhstan	Grassland, floodplain	Region	1999	Breeding season
13	Thiollay (2007a)	Burkina Faso	Sudan savanna, grassland, floodplain, woodland, protected area	Region	2004–2005	Dry
14	Weesie and Belemsogbo (1997)	Burkina Faso	Sudan savanna, protected area	Local	1991–1992	Dry
15	Thiollay (1975b)	Ivory Coast	Guinea savanna, protected area	Local	1968–1973	Dry
16	Thiollay (1975b)	Ghana	Guinea savanna, protected area	Local	1972	Dry
17	Ogada and Keesing (2010)	Kenya	Savanna woodland, protected area	Local	2001–2003	Dry and wet
18	Ogada et al. (2010)	Kenya	Savanna woodland, protected area	Region	2010	Dry
19	Njilima et al. (2010)	Tanzania	Savanna woodland, protected area	Region	2010	Dry
20	Thiollay et al. (2008)	Tanzania	Savanna woodland, protected area	Region	2008	Dry

Table 4 continued

Number	References	Country	Habitat	Coverage[a]	Years	Season
21	Sorley and Andersen (1994)	Kenya	Savanna woodland, protected area	Local	1990	Dry
22	Thiollay (1970)	Senegal	Sudan savanna, protected area	Local	1969	Dry
23	Barkhuysen (2004)	South Africa	Grassland, agriculture, forest, protected area	Region	2003	Summer

[a] Region: transects covered region within a country or multiple countries; local: transects covered single protected areas, with or without buffer zones

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